still decline to come in to the reservations and keep up their old semi-nomadic life in the mountains.

As to the social organization of the Heiltsuk it was found that the tribe contains four clans—the eagle, wolf, raven and killer whale. There is nothing corresponding to the phratries of tribes farther north, but the individual clans are strictly exogamous, and marriage is also forbidden with members of corresponding clans in certain other tribes. Descent is mixed, maternal and paternal, but preference is shown for the clan of the mother. In the case of a single child it almost invariably takes the maternal clan. There were formerly three social classes—nobility, common people and slaves. The nobility or chiefs were of different ranks, higher position being obtained by means of the potlatch. A member of the lower classes, however, could never obtain nobility.

A very considerable number of specimens were collected by the expedition which will materially increase the scientific value of the collections from the North Pacific coast in the American Museum of Natural History. The new material consists mainly of archæological collections from Kamloops, Lytton and Port Hammond; an ethnological collection from Spence's Bridge, another one from Chilcotin Valley. From the northern part of the coast a very full collection of masks and carvings illustrating mythology of the Bella Coola was obtained. Another collection illustrates the arts and ceremonials of the Kwakiutl and of the Nootka. Finally the large collection of casts and photographs of Indians must be mentioned.

Ethnology is deeply indebted to Dr. Jesup for inaugurating this important investigation, which, we may hope, will help to settle finally a number of the most difficult problems regarding the early history of mankind.

*EXPERIMENTAL MORPHOLOGY.**

IN looking at the progress which has been made in the study of plant morphology I have been as much impressed with the different attitudes of mind toward the subject during the past 150 years as by the advance which has taken place in methods of study and the important acquisitions to botanical science. These different view points have coincided to some extent with distinct periods of time. What Sachs in his 'History of Botany' calls the 'New Morphology' was ushered in near the middle of the present century by Von Mohl's researches in anatomy, by Naegeli's investigation of the cell and Schleiden's history of the development of the flower. The leading idea in the study of morphology during this period was the inductive method for the purpose of discerning fundamental principles and laws, not simply the establishment of individual facts, which was especially characteristic of the earlier period when the dogma of the constancy of species prevailed.

The work of the 'herbalists' had paved the way for the more logical study of plant members by increasing a knowledge of species, though their work speedily degenerated into mere collections of material and tabulations of species with inadequate descriptions. Later the advocates of metamorphosis and spiral growth had given an impetus more to the study of nature, though diluted with much poetry and too largely subservient to the imagination or idealistic notions.

But it was reserved for Hoffmeister,† whose work followed within three decades of the beginnings of this period, to add to the

*Address of the Vice-President before Section G—Botany—of the American Association for the Advancement of Science, Detroit, 1897.

† Bibliographical details will be appended when the address is published in the Proceedings of the Association.

inductive method of research as now laid down the comparative method, and extending his researches down into the Pteridophyta and Bryophyta, he not only established for these groups facts in sexuality which Camerarius and Robert Brown had done for the Spermatophyta, but he did it in a far superior manner. He thus laid the foundation for our present conceptions of the comparative morphology of plants. Naegeli's investigations of the cell had emphasized the importance of its study in development and now the relation of cell growth to the form of plant members was carried to a high degree, and an attempt was made to show how dependent the form of the plant was on the growth of the apical cell in the Pteridophyta and Bryophyta, though later researches have modified this view, and how necessary a knowledge of the sequence of cell division was to an understanding of homologies and relationships. Thus in developmental and comparative studies morphology has been placed on a broader and more natural basis, and the homologies and relationships of organs between the lower and higher plants are better understood.

But the growth of comparative morphology has been accompanied by the interpretation of structures usually from a teleological standpoint, and in many cases with the innate propensity of the mind to look at nature in the light of the old idealistic theories of metamorphosis.

I wish now to enquire if we have not recently entered upon a new period in our study of comparative morphology. There are many important questions on which comparative studies of development under natural or normal conditions alone cannot afford a sufficient number of data. We are constantly confronted with the problems of the interpretation of structure and form, not only as to how it stands in relation to structures in other plants which we deal with in comparative morphology, but the meaning of the structure or form itself, and in relation to the other structures of the organism, in relation to the environment and in relation to the past. This must be met by an enquiry on our part as to why the structure or form is what it is, and what are the conditions which influence it. This we are accustomed to do by *experiment*, and it begins to appear that our final judgments upon many questions of morphology, especially those which relate to variation, homology, etc., must be formed after the evidence is obtained in this higher trial court, that of *experimental morphology*. While experimental morphology as a designation of one branch of research in plants, or as a distinct and important field of study, is not yet fully taken cognizance of by botanists, we have only to consult our recent literature to find evidence that this great and little explored field has already been entered upon.

Experimental methods of research in the study of plants have been in vogue for some time, but chiefly by plant physiologists and largely from the standpoint of the physical and chemical activities of the plant, as well as those phases of nutrition and irritability, and of histologic structure, which relate largely to the life processes of the plants, and in which the physiologist is therefore mainly interested. In recent years there has been a tendency in physiological research to limit the special scope of these investigations to those subjects of a physical and chemical nature. At the same time the study of the structure and behavior of protoplasm is coming to be regarded as a morphological one, and while experimental methods of research as applied to the morphology of protoplasm and the cell is comparatively new there is already a considerable literature on the subject, even from the side of plant organisms (Davenport, '97). While certain of the

phenomena of irritability and growth are closely related to the physics of plant life, they are essentially morphologic, and it is here especially that we have a voluminous literature based strictly on the inductions gained by experimentation, and for which we have chiefly to thank the plant physiologists.

If we were to write the full history of experimental morphology in its broadest aspects we could not omit those important experimental researches on the lower plants in determining the ontogeny of polymorphic species among the algæ and fungi which were begun so ably by DeBary, Tulasne, Pringsheim and others and carried on by a host of European and American botanists. The tone which these investigations gave to taxonomic botany has been felt in the study of the higher plants, by using to some extent the opportunities at botanic gardens, where plants of a group may be grown under similar conditions for comparison, and in the establishment of alpine, subalpine and tropical stations for the purpose of studying the influence of climate on the form and variations of plants, and in studying the effect of varying external conditions.

While experimental morphology in its broadest sense also includes in its domain cellular morphology and the changes resulting from the directive or taxic forces accompanying growth, it is not these phases of morphology with which I wish to deal here.

The question is rather that of experimental morphology as applied to the interpretation of the modes of progress followed by members and organs in attaining morphologic individuality, in the tracing of homologies, in the relation of members associated by antagonistic or correlative forces, the dependence of diversity of function in homologous members on external and internal forces, as well as the causes which determine the character of certain paternal or maternal structures. I shall deal more especially with the experimental evidence touching the relation of the members of the plant which has been represented under the concept of the leaf as expressed in the metamorphosis theory of the idealistic morphology. The poetry and mystery of the plant world, which was so beautifully set forth in the writings of Goethe and A. Braun, are interesting and entrancing, and the poetic communication with nature is elevating to our ethical and spiritual natures. But fancy or poetry cannot guide us safely to the court of inquiry. We must sometimes lay these instincts aside and deal with nature in a cold, experimental, calculating spirit.

The beginnings of experimental morphology were made about one century ago, when Knight, celebrated also for the impulse which he gave to experimental physiology, performed some very simple experiments on the potato plant. The underground shoots and tubers had been called roots until Hunter (77) pointed out the fact that they were similar to stems. Knight tested the matter by experiment, and demonstrated that the tubers and undergound stems could be made grow into aërial leafy shoots. This he regarded as indicating a compensation of growth, and he thought farther that a compensation of growth could be shown to exist between the production of tubers and flowers on the potato plant. He reasoned that by the prevention of the development of the tubers the plant might be made to bloom. An early sort of potato was selected, one which rarely or never set flowers, and the shoots were potted with the earth well heaped up into a mound around the end of the shoot. When growth was well started the soil was washed away from the shoot and the upper part of the roots so that the plant was only connected with the soil by the roots. The

tubers were prevented from growing and numbers of flowers were formed. This result he also looked upon as indicating a compensation of growth between the flowers and tubers. While we recognize Knight's experiments as of great importance, yet he erred in his interpretation of the results of this supposed correlation between the tubers and flowers, as Vöchting has shown. By repeating Knight's experiment, and also by growing shoots so that tubers would be prevented from developing, while at the same time the roots would be protected, flowers were obtained in the first case while they were not in the second, so that the compensation of growth, or correlation of growth, here exists between the vegetative portion of the plant and the flowers instead of between the production of tubers and flowers as Knight supposed.

The theory of metamorphosis as expressed by Goethe and A. Braun ('51) and applied to the leaf regarded the leaf as a *concept* or *idea*. As Goebel ('80) points out, Braun did not look upon any one form as the typical one which through transformation had developed the various leaf forms, but each one represented a wave in the march of the successive billows of a metamorphosis, the shoot manifesting successive repetitions or renewals of growth each season, presenting in order the 'niederblätter, laubblätter, hochblätter, kelchblätter, blumenblätter, staubblätter, fruchtblätter. Though it had been since suggested from time to time, as Goebel ('80) remarks, that the foliage leaf must be regarded as the original one from which all the other forms had arisen (though at that time Goebel did not think this the correct view), no research, he says, had been carried on, not even in a single case to determine this point. Goebel plainly showed in the case of *Prunus padus* that axillary buds which under normal conditions were formed one year with several bud scales could be made by artificial treatment to develop during the first year. This he accomplished by removing all the leaves from small trees in April, and in some cases also cutting away the terminal shoot. In these cases the axillary shoot, instead of developing a bud which remained dormant for one year as in normal cases, at once began to grow and developed well-formed shoots. Instead of the usual number of bud scales, there were first two stipule-like outgrowths, and then fully expanded leaves were formed, so that in this case, he says, the metamorphosis of the leaf to bud scales was prevented. For this relation of bud scales to foliage leaves Goebel proposed the term 'correlation of growth' ('80). In the case of *Vicia faba* removal of the lamina of the leaf of seedlings when it was very young caused the stipules to attain a large size and to perform the function of the assimilating leaf. He here points out that experimentation aids us in interpreting certain morphological phenomena which otherwise might remain obscure. He cites the occasional occurrence (Moquin-Tandon) in the open of enlarged stipules of this plant which his experiment aids in interpreting. In the case of *Lathyrus aphaca* the stipules are large and leaf-like, while he part which corresponds to the lamina of the leaf is in the form of a tendril, the correlation processes here having brought about the enlargement of the stipules as the lamina of the leaf became adapted to another function. Kronfeld ('86, '87) repeated some of Goebel's experiments, obtaining the same results, and extended them to other plants (*Pirus malus* and *Pisum sativum*), while negative results attended some other experiments. Hildebrand, in some experiments on seedlings and cuttings, found that external influences affected the leaves, and in some cases, where the cotyledons were cut, foliage leaves appeared in place of the usual bud scales, and in *Oxalis rubella* removal of the

foliage leaf, which appears after the cotyledons, caused the first of the bulb scales, which normally appear following the foliage leaf, to expand into a foliage leaf.

In some experiments on the influence of light on the form of the leaves Goebel ('96) has obtained some interesting results. Plants of *Campanula rotundifolia* were used. In this species the lower leaves are petioled and possess broadly expanded, heart-shaped laminæ, while the upper leaves are narrow and sessile, with intergrading forms. Plants in different stages of growth were placed in a poorly-lighted room. Young plants which had only the round leaves under these conditions continued to develop only this form of leaf, while older plants which had both kinds of leaves when the experiment was started now developed on the new growth of the shoot the round-leaved form. In the case of plants on which the flower shoot had already developed, side shoots with the round leaves were formed. Excluding the possibility of other conditions having an influence here, the changes in the form of the leaves has been shown to be due to a varying intensity of light. The situation of the plants in the open favor this view, since the leaves near the ground in these places are not so well lighted as the leaves higher up on the stem. In this case the effect of dampness is not taken into account by the experimenter, and, since dampness does have an influence on the size of the leaf, it would seem that it might be at least one of the factors here. An attempt was now made to prevent the development of the round leaves on the young seedlings. For this purpose the germinating seeds were kept under the influence of strong and continuous lighting. The round leaves were nevertheless developed in the early stage, an indication that this form of the leaf on the seedling has become fixed and is hereditary. Hering ('96) found that enclosing the larger cotyledon of *Streptocarpus* in a plaster cast, so as to check the growth, the smaller and usually fugacious one grew to the size of the larger one, provided the experiment was started before the small one was too old. Amputation of the large cotyledon gave the same results.

Other experimenters have directed their attention to the effect of light and gravity on the arrangement of the leaves on the stem, as well as the effect of light on the length of the petioles and breadth of the lamina. Among these may be mentioned the work of Weisse ('95), Rosenvinge ('94), and others.

Goebel has shown experimentally that dampness is also one of the external influences which can change the character of xerophyllous leaves. A New Zealand species of *Veronica* of xerophyllous habit and scaly appressed leaves in the seedling stage has spreading leaves with a broad lamina. Older plants can be forced into this condition in which the leaves are expanded by growing them in a moist vessel ('96). Gain, Askenasy and others have shown that dampness or dryness has an important influence in determining the character of the leaves.

The results of the experiments in showing the relation of the leaf to the bud scales Goebel regards as evidence that the foliage leaf is the original form of the two, and that the bud scale is a modification of it.

Treub ('72) conducted some interesting experiments for the purpose of determining the homology of the pappus of the Compositæ. Gall-insects were employed to stimulate the pappus of *Hieracium umbellatum*, and it was made to grow into a normal calyx with five lobes. (A recent letter from Professor Treub states that he later repeated these experiments with other species of Compositæ with like results, but the work was not published.) Kny ('94) found in seedlings and cuttings which he experimented with that, while there was still

stored food available for the roots and shoots, there was little, if any, dependence of one upon the other. Hering ('96) comes to somewhat different conclusions as a result of his experiments, finding that in some cases there was a slight increase of growth, while in others growth of the one was reciprocally retarded when the other was checked in development. Numerous cases of horticultural practice in pollination of fruits show that the form and size of the fruit and of the adjacent parts, as well as the longer or shorter period of existence of the floral envelopes, can be influenced by pollination.

The investigations carried on by Klebs ('96) in the conjugation of *Spirogyra* suggest how experimentation of this kind may be utilized to determine questions which in special cases cannot be arrived at easily by direct investigation. If threads of *Spirogyra varians* which are ready for conjugation are brought into a (0.5%) solution of agar-agar, in such a way that nearly parallel threads lie at a varying distance in their windings, where they are within certain limits, the conjugation tubes are developed and the zygospores are formed; but where the threads lie at too great a distance for the influence to be exerted, the cells remain sterile, and no conjugation tubes are developed. If, now, these threads be brought into a nutrient solution, these cells, which were compelled to remain sterile, grow and develop into new threads, *i. e.*, they take on the vegetative, though they are fully prepared for the sexual function. Strasburger ('97) has pointed out that this may be taken as excluding the possibility of there being a reducing division of the chromosomes during the maturing of the sexual cells, a process which takes place in animals, and that the behavior of *Spirogyra* in this respect agrees with what is known to take place in the higher plants, viz., that the reduction process is not one which is concerned in the maturity of the gametes. The same could be said of *Polyphagus*, in which Nowakowski ('78) found that before the zygospore was completely formed the protoplasm moved out and formed a new sporangium.

In the case of *Protosiphon botryoides* Klebs was also able to compel the parthenogenetic development of the motile gametes, and the same thing was observed in the case of the gametes of *Ulothrix*. If we are justified in interpreting this phenomenon as Strasburger suggests, the evidence which Raciborski ('96) gives as a result of his experiments with *Basidiobolus ranarum* would support the idea that there is no reducing division in the chromosomes before the formation of the nuclei of the gametes. Raciborski found that in the case of the young zygospores of this plant, in old nutrient medium where the fusion of the plasma contents had taken place, but before the nuclei had fused, if they were placed in a fresh nutrient medium the fusion of the nuclei was prevented, and vegetative growth took place, forming a hypha which possessed two nuclei, the paternal one and the maternal one. Raciborski interprets Eidam's ('87) study of the nuclear division prior to the copulation of the gametes as showing that the reducing division takes places here as in the maturation of the sexual cells of animals, and looks upon the premature germination of the zygospore as showing that a paternal and maternal nucleus possesses the full peculiarities of a normal vegetative one. However, we are not justified in claiming a reducing division for the nuclei preceding the formation of the gametes in *Basidiobolus* from the work of Eidam, since he was not able to obtain sufficiently clear figures of the division to determine definitely how many divisions took place, to say nothing of the lack of definite information as to the number of chromosomes. Fairchild ('96)

has recently studied more carefully the nuclear division, but on account of the large number of the chromosomes was not able to determine whether or not a reduction takes place. He points out, as others have done, the similarity in the process of the formation of the conjugating cells of *Basidiobolus* and *Mougeotia* among the *Mesocarpeæ*, and to these there might be added the case of *Sirogonium* in which the paternal cell just prior to copulation undergoes division. The division of the copulation cell in *Basidiobolus*, *Mougeotia*, *Sirogonium*, etc., suggest at least some sort of preparatory act, but whether this is for the purpose of a quantitative reduction of the kinoplasm, as Strasburger thinks sometimes takes place, or is a real reduction in the number of the chromosomes, must be determined by further study, so that the bearing of these experiments on the question of a reducing division must for the time be held in reserve.

One of the very interesting fields for experimental investigation is that of the correlation processes which govern the morphology of the sporophylls (stamens and pistils) of the Spermatophyta. One of the controlling influences seems to be that of nutrition, and in this respect there is some comparison to be made with the correlative processes which govern the determination of sex in plants.

Among the ferns and some others of the Pteridophyta a number of experiments have been carried on by Prantl, Bauke, Heim ('96), Buchtien ('87) and others to determine the conditions which influence the development of antheridia and archegonia. Prantl found that in prothallia of the ferns grown in solutions lacking nitrogen there was no meristem and consequently no archegonia, while antheridia were developed, but if the prothallia were changed to solutions containing nitrogen, meristem and archegonia were developed. All the experiments agree in respect to nutrition; with scanty nutrition antheridia only were developed, while with abundant nutriment archegonia were also developed. Heim studied the influence of light and found that fern prothallia grow best with light of 20%–25%. Exclusion of the ultra violet rays does not affect the development of the sexual organs. He argues from this that the ultra violet rays are not concerned in the elaboration of the material for flower production as Sachs had suggested. In yellow light the prothallia grew little in breadth; they also grew upward, so that few of the rhizoids could reach the substratum. Antheridia were here very numerous. After seven months these prothallia were changed to normal light, and in four months afterward archegonia were developed.

Among the algæ Klebs ('96) has experimented especially with *Vaucheria*, such species as *V. repens* and *V. ornithocephala*, where the antheridia and oogonia are developed near each other on the same thread. With weak light, especially artificial light, the oogonium begins first to degenerate. He never succeeded in suppressing the antheridia and at the same time in producing oogonia.

High temperature, low air pressure or weak light tend to suppress the oogonia, and at the same time the antheridia may increase, so that the number in a group is quite large, while the oogonium degenerates or develops vegetatively. Klebs concludes from his experiments that the causes which lie at the bottom of the origin of sex in *Vaucheria*, as in other organisms, are shrouded in the deepest mystery. In the higher plants a number of experiments have been carried on for the purpose of learning the conditions which govern the production of staminate and pistillate flowers, or, in other words, the two kinds of sporophylls. From numerous empirical observations on

diœcious Spermatophyta, the inference has generally been drawn that nutrition bears an important relation to the development of the staminate and pistillate flowers; that scanty nutrition produces a preponderance of staminate plants, while an abundance of nutrition produces a preponderance of pistillate plants. For a period covering three decades several investigators have dealt with this question experimentally, notably K. Müller ('64), Haberlandt ('75, '77) and Hoffmann ('85). These experiments in general give some support to the inferences from observations, yet the results indicate that other influences are also at work, for the ratios of preponderance either way are not large enough to argue for this influence alone. In a majority of cases thick sowings, which in reality correspond to scanty nutrition, tend to produce staminate plants; while thin sowings tend to produce pistillate plants. In the case of the hemp (*Cannabis sativa*) Hoffmann found that these conditions had practically no influence. He suggests that the character of each may have been fixed during the development of the seed, or even that it may be due to late or early fecundation ('71).

In monœcious plants it has often been observed that pistillate flowers change to staminate ones and *vice versa*, and in diœcious plants pistillate ones sometimes are observed to change to staminate ones (the hemp, for example; see Nagel, 1879). K. Müller ('64) states that by scanty nutrition the pistillate flowers of *Zea mays* can be reduced to staminate ones.

Among the pines what are called androgynous cones have in some instances been observed. In *Pinus rigida* and *P. thunbergii*, for example, they occur (Masters ('68). Matsuda ('92) has described, in the case of *Pinus densiflora* of Japan, pistillate and androgynous flowers, which developed in place of the staminate flowers, and conversely staminate and androgynous flowers in place of pistillate ones. Fujii ('95) has observed that where the pistillate or androgynous flowers of *Pinus densiflora* occur in place of the staminate ones they are usually limited to the long shoots which are developed from the short ones of the previous year. The proximity of these transformed short shoots (Kurztriebe) to injuries of the long ones suggested that the cutting away of the long ones might induce the short ones to develop into long ones and the flowers which were in the position for staminate ones to become pistillate.

Fujii says: "In fact, the injuries producing such effect are frequently given by Japanese gardeners to the shoots of the year of *Pinus densiflora* in their operations of annual pollarding. But the 'Langtrieb' which is transformed from a 'Kurztrieb' of the last year does not necessarily bear female or hermaphrodite flowers in the positions of male flowers." To determine the influence of pollarding of the shoots he carried on experiments on this pine in the spring of 1895. He pollarded the shoots, so as, as he terms it, to induce the nourishment to be employed in the development of the flowers and short shoots near the seat of injury; in other cases one or two shoots were preserved, while all the adjacent shoots of last year's growth at the top of the branch were removed, and, farther, both of these processes were combined. Out of the 45 branches experimented on, and on which there were no signs of previous injury, there were nine pistillate or androgynous flowers in place of staminate ones; in 21 branches with signs of previous injury five were transformed, while in 2,283 not experimented on, and with no signs of previous injury, only seven were transformed. Such abnormal flowers, then, are due largely to the injuries upon the adjacent shoots, and, Fujii thinks, largely to the increased amount of nourishment which is conveyed to them as a result of this.

From the experiments thus far conducted upon the determination of sex in plants or upon the determination of staminate or pistillate members of the flowers, nutrition has at least some influence in building up the nourishing tissue for the two different organs or members. This can in part be explained on the ground that antheridia and staminate members of the plant are more or less short lived in comparison with the archegonia and pistillate members, the latter requiring more bulk of tissue to serve the purpose of protection and nourishment to the egg and embryo. It is thus evident that while some progress has been made in the study of this question we are far from a solution of it. Experiment has proceeded largely from a single standpoint, viz., that of the influence of nutrition. Other factors should be taken into consideration, for there are evidently other external influences and internal forces which play an important rôle, as well as certain correlation processes, perhaps connected with the osmotic activities of the cell sap.

The relation of the parts of the flower to the foliage leaves is a subject which has from time to time called forth discussion. That they are but modifications of the foliage leaf, constituents of the leaf concept, is the contention of the metamorphosis theory, and that the so-called sporophylls are modified foliage leaves, is accepted with little hesitation by nearly all botanists, though it would be very difficult, it seems to me, for any one to present any very strong argument from a phylogenetic standpoint in favor of the foliage leaf being the primary form in its evolution on the sporophyte, and that the sporophyll is a modern adaptation of the foliage leaf. Numerous cases are known of intermediate forms between sporophylls and foliage leaves both in the Spermatophyta and Pteridophyta. These are sometimes regarded as showing reversion, or indicating atavism, or in the case of some of the ferns as being contracted and partially fertile conditions of the foliage leaf. There has been a great deal of speculation regarding these interesting abnormal forms, but very little experimentation to determine the causes or conditions which govern the processes.

In 1894 I succeeded in producing a large series of these intermediate forms in the sensitive fern (*Onoclea sensibilis*). The experiments were carried on at the time for the especial purpose of determining whether in this species the partially developed sporophyll could be made to change to a foliage leaf and yet possess characters which would identify it as a transformed sporophyll. The experiments were carried on where there were a large number of the fern plants. When the first foliage leaves were about 25 cm. high they were cut away (about the middle of May). The second crop of foliage leaves were also cut away when they were about the same height during the month of June. During July, in which time the uninjured ferns were developing the normal sporophylls, those which were experimented upon presented a large series of gradations between the normal sporophyll and fully expanded foliage leaves. Among these examples there are all intermediate stages from sporophylls which show very slight expansions of the distal portion of the sporophyll and the distal portions of the pinnæ, until we reach forms which it is very difficult to distinguish from the normal foliage leaf. Accompanying these changes are all stages in the sterilization of the sporangia (and the formation of prothalloid growths), on some more broadly expanded sporophylls there being only faint evidences of the indusia.

The following year (1895) similar experiments were carried on with the ostrich fern (*Onoclea struthiopteris*) and similar results were obtained. At the time that these experiments were conducted I was unaware of

the experiments performed by Goebel on the ostrich fern. The results he reached were the same; the sporophyll was more or less completely transformed to a foliage leaf. Goebel regards this as the result of the correlation processes, and looks upon it as indicating that the sporophyll is a transformed foliage leaf, and that the experiment proves the reality here of the modification which was suggested in the theory of metamorphosis, and thus the foliage leaf is looked upon by him as the primary form. Another interpretation has been given to these results, viz., that they strengthen the view that the sporophyll, from a phylogenetic standpoint, is primary, while the foliage leaf is secondary. What one interprets as a reversion another regards as indicating a mode of progress in the sterilization of potentially sporogenous tissue and its conversion into assimilatory tissue. It is, perhaps, rather to be explained by the adaptive equipoise of the correlative processes existing between the vegetative and fruiting portions of the plant, which is inherited from earlier times. Rather when spore production appears on the sporophyte could this process be looked upon as a reversion to the primary office of the sporophyte, so that in spore production of the higher plants we may have a constantly recurring reversion to a process which in the remote past was the sole function of this phase of the plant. In this way might be explained those cases where sporangia occur on the normal foliage leaf of *Botrychium*, and some peculiar cases which I have observed in *Osmunda cinnamomea*. In some of the examples of this species it would appear that growth of the leaf was marked by three different periods even after the fundament was outlined, the first a vegetative, second a spore-producing, and third a vegetative again; for the basal portions of the leaf are expanded, the middle portions spore-bearing, the passage into the middle portions being gradual, so that many sporangia are on the margins of quite well-developed pinnæ. These gradations of the basal part of the leaf, and their relation to the expanded vegetative basal portion, showing that the transition here has been from partially formed foliage leaf to sporophyll after the fundament was established, and later the increments of the vegetative part from the middle toward the terminal portion, as shown by the more and more expanded condition of the lamina and decreasing sporangia, indicate that vegetative forces are again in the ascendency. This suggests how unstable is the poise between the vegetative leaf and sporophyll in structure and function in the case of this species.

For two successive years I have endeavored by experiment to produce this transformation in *Osmunda cinnamomea*, but thus far without sufficiently marked results. The stem of the plant is stout, and this, together with the bases of the leaves closely overlapping, contains considerable amounts of stored nutriment, which make it difficult to produce the results by simply cutting off the foliage leaves. The fact that these transformations are known to occur where fire has overspread the ground, and, as I have observed, where the logging in the woods seriously injured the stools of the plant, it would seem that deeper seated injuries than the mere removal of foliage leaves would be required to produce the transformation in this species. It may be that such injury as results from fire or the severe crushing of the stools of the plant would be sufficient to disturb the equilibrium which existed at the time, that the action of the correlative forces is changed thereby, and there would be a tendency for the partially developed foliage leaves to form sporangia, then when growth has proceeded for a time this balance is again changed.

The theory that the foliage leaves of the

sporophyte have been derived by a process of sterilization, and that the transformation of sporophylls to foliage leaves in an individual indicates the mode of progress in this sterilization, does not necessarily involve the idea that the sporophyll of any of the ferns, as they now exist, was the primary form of the leaf in that species, and that by sterilization of some of the sporophylls, the present dimorphic form of the leaves was brought about. The process of the evolution of the leaf has probably been a gradual one and extends back to some ancestral form now totally unknown. One might differ from Professor Bower in the examples selected by him to illustrate the course of progress from a simple and slightly differentiated sporophyte to that exhibited in the various groups of the Pteridophyta, but it seems to me that he is right in so far as his contention for the evolution of vegetative and assimilatory members of the sporophyte can be illustrated by a comparison of the different degrees of complexity represented by it in different groups, and that this illustrates the mode of progress, as he terms it, in the sterilization of potential sporangenous tissue.

On this point it appears that Professor Bower has been unjustly criticised. The forms selected to illustrate his theory were chosen not to represent ancestral forms, or direct phylogenetic lines, but solely for the purpose of illustrating the gradual transference of spore-bearing tissue from a central to a peripheral position, and the gradual eruption and separation of spore-bearing areas, with the final sterilization of some of these outgrowths.

To maintain that in phylogeny the sporophyll is a transformed foliage leaf would necessitate the predication of ancestral plants with only foliage leaves, and that in the case of these plants the vegetative condition of the sporophyte was the primary one, spore production being a later developed function. Of the forms below the Pteridophyta, so far as our present evidence goes, the sporophyte originated through what Bower calls the gradual elaboration of the zygote. All through the Bryophyta, wherever a sporophyte is developed, spore production constantly recurs in each cycle of the development, and yet there is no indication of any foliar organs on the sporophyte. The simplest forms of the sporophyte contain no assimilatory tissue, but in the more complex forms assimilatory tissue is developed to some extent, showing that the correlative forces which formerly were so balanced as to confine the vegetative growth to the gametophyte, and fruiting to the sporophyte, are later changing; that vegetative growth and assimilation are being transferred to the sporophyte, while the latter still retains the function of spore production, though postponed in the ontogeny of the plant.

If we cannot accept some such theory for the origin of sporophylls and foliage leaves by gradual changes in potentially sporogenous tissue somewhat on the lines indicated by Bower, it seems to me it would be necessary, as already suggested, to predicate an ancestral form for the Pteridophyta in which spore production was absent. That is, spore production, in the sporophyte of ancestral forms of the Pteridophyta, may never have existed in the early period of its evolution and spore production may have been a later development. But this, judging from the evidence which we have, is improbable, since the gametophyte alone would then be concerned in transmitting hereditary characters, unless the sporophyte through a long period developed the gametophyte stage through apospory. Bower says in taking issue with Goebel's statement that the experiments on Onoclea prove the sporophyll to be a transformed foliage leaf: "I assert, on the other hand, that this is not proved, and that a good

case could be made out for priority of the sporophyte; in which event the conclusion would need to be inverted, *the foliage leaf would be looked upon as a sterilized sporophyll.* This would be perfectly consistent with the *correlation* demonstrated by Professor Goebel's experiments, as also with the intercalation of a vegetative phase between the zygote and the production of spores." In another place he says: "To me, whether we take such simple cases as the Lycopods or the more complex case of the Filicineæ, the sporangium is not a gift showered by a bountiful Providence upon pre-existent foliage leaves; the sporangium, like other parts, must be looked upon from the point of view of descent; its production in the individual or in the race may be deferred, owing to the intercalation of a vegetative phase, as above explained; while, in certain cases at least, we probably see in the foliage leaf the result of the sterilization of sporophylls. If this be so, much may be then said in favor of the view that the appearance of sporangia upon the later formed leaves of the individual is a reversion to a more ancient type rather than a metamorphosis of a progressive order."

As I have endeavored to point out in another place, if a disturbance of these correlative processes results in the transference of sporophyllary organs to vegetative ones on the sporophyte "why should there not be a similar influence brought to bear on the sporophyte, when the same function resides solely in the gametophyte, and a disturbing element of this kind is introduced? To me there are convincing grounds for believing that this influence was a very potent, though not the only one in the early evolution of sporophytic assimilatory organs. By this I do not mean that in the Bryophyta, for example, injury to the gametophyte would now produce distinct vegetative organs on the sporophyte, which would tend to make it independent of the gametophyte. But that in the bryophyte-like ancestors of the pteridophytes an influence of this kind did actually take place, appears to me reasonable.

"In the gradual passage from an aquatic life, for which the gametophyte was better suited, to a terrestrial existence, for which it was unadapted, a disturbance of the correlative processes was introduced. This would not only assist in the sterilization of some of the sporogenous tissue, which was taking place, but there would also be a tendency to force this function on some of the sterilized portions of the sporophyte, and to expand them into organs better adapted to this office. As eruptions in the mass of sporogenous tissue took place and sporophylls were evolved, this would be accompanied by the transference of the assimilatory function of the gametophyte to some of these sporophylls."

Because sporophytic vegetation is more suited to dry land conditions than the gametophytic vegetation, it has come to be the dominating feature of land areas. Because the sporophyte in the Pteridophyta and Spermatophyta leads an independent existence from the gametophyte, it must possess assimilatory tissue of its own, and this is necessarily developed first in the ontogeny, but it does not necessarily follow, therefore, that the foliage leaf was the primary organ in the phylogeny of the sporophyte. The provision for the development of a large number of spores in the thallophytes, so that many may perish and still some remain to perpetuate the race, is laid hold on by the bryophytes where the mass of spore-bearing cells increases and becomes more stable, for purposes of the greatest importance. Instead of perishing, some of the sporogenous tissue forms protecting envelopes, then supporting and conducting tissue, and finally, in the pteridophytes and spermatophytes, nutritive and assimilatory structures are developed. Nature is prodi-

gal in the production of initial elementary structures and organs. But while making abundant provision for the life of the organism through the favored few, she has learned to turn an increasing number of the unfavored ones to good account. Acted upon by external agents and by internal forces, and a changing environment, advance is made step by step to higher, more stable and prolonged periods.

While we have not yet solved any one of these problems, the results of experimental morphology are sufficient to indicate the great importance of the subject and the need of fuller data from a much larger number of plants. If thus far the results of experiments have not been in all cases sufficient to overthrow the previous notions entertained touching the subjects involved, they at least show that there are good grounds for new thoughts and new interpretations, or for the amendment of the existing theories. While there is not time for detailing, even briefly, another line of experiment, viz, that upon leaf arrangement, I might simply call attention to the importance of the experiments conducted by Schumann and Weisse from the standpoint of Schwendener's mechanical theory of leaf arrangement ('78). Weisse ('94) shows that the validity of the so-called theory of the spiral arrangement of the leaves on the axis may be questioned, and that there are good grounds for the opening of the discussion again. It seems to me, therefore, that the final judgment upon either side of all these questions cannot now be given. It is for the purpose of bringing fresh to the minds of the working botanists the importance of the experimental method in dealing with these problems of nature that this discussion is presented as a short contribution to the subject of experimental morphology of plants.

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PHYSIOLOGY AT THE BRITISH ASSOCIATION.

DURING the Toronto meeting of the British Association for the Advancement of Science the Section in Physiology held seven sessions under the presidency of Professor Michael Foster (Cambridge). The sessions were held in the Biological Building of the University of Toronto, and forty-one papers and demonstrations were presented. The proceedings began upon Thursday, August 19th, with the admirable address of the President, which will be printed in a future number of SCIENCE. The sectional papers of that day related in general to the subject of motion. Professor H. P. Bowditch (Harvard) discussed the rhythm of smooth muscles. Rings from the frog's stomach, when suspended, exhibit sooner or later spontaneous contractions, which continue for from forty-five minutes to twenty-four hours. The graphic curve of such contractions seems to be compound, being formed by the superposition of two waves, which represent two rhythmic contractions of different rates. Sets of contractions are also repeated rhythmically. Professor G. C. Huber (Michigan) gave the results of further researches on the innervation of motor tissues with especial reference to nerve-endings in the sensory muscle-spindles. The main points in this paper are given in SCIENCE, Vol. V., p. 908. Mr. O. F. F. Grünbaum (Cambridge) demonstrated by lantern slides the muscle-spindles in pathological conditions. Professor F. S. Lee (Columbia) discussed the ear and the lateral line in fishes. These two organs are equilibrative in function, and the former is probably the phylogenetic derivative of the latter. Audition in the customary sense of the word is wanting in fishes, and first appears with the change from an aquatic to a land existence. Professor W. P. Lombard (Michigan) spoke on the effect of the frequency of excitations on the contractility of muscles. Dr. J. H.